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BIOLOGY OF THE GOLDENROD GALL-MAKER GNORIMOSCHEMA GALLÆSOLIDAGINIS RILEY.[1]

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RALEIGH, N. C.

INTRODUCTION.

While engaged during the past seven years in tracing the polyembryonic development of a hymenopterous parasite *Copidosoma gelechiæ* How., the writer has of necessity followed through several of these years the life-history of its host *Gnorimoschema gallæsolidaginis* Riley, the maker of an elliptical gall on the stems of goldenrod. This study has revealed several striking points in the biology of an insect whose gall has long been familiar to many naturalists. Certain seasonal data have also been secured in the widely separated States of Vermont, New York, and North Carolina, which indicate quite an interesting variation in the time of appearance and length of the different stages in the regions mentioned.

HISTORY AND DISTRIBUTION.

The maker of the elliptical gall of the goldenrod is the larva of a moth belonging to the family Gelechiidæ. It was described by C. V. Riley[2] in 1869 from specimens bred in Missouri and named *Gelechia gallæsolidaginis*, and at this time Riley also published some notes

[1] Contribution from the entomological laboratories of Cornell University and Experiment Station of the North Carolina Department of Agriculture.

[2] Riley, C. V., Mo. Rept. State Entomologist Nox. Insects, 1. 1869, p. 173.

on the larva and its gall. Busck[1] in 1900 placed the species in a new genus *Gnorimoschema* and called *gallæsolidaginis* the type. Since then the species has been rather frequently referred to by naturalists so that its distribution is known to include the States of Colorado, Missouri, Minnesota, Michigan, Vermont, Massachusetts, Connecticut, New York, Pennsylvania, New Jersey, Maryland, District of Columbia, Virginia and North Carolina, and will probably be found to occur in the neighboring states. The life-history is therefore known in a general way although the few references concerned contain some conflicting statements particularly regarding the adult and its habits.

The life-history of a closely related species *Gnorimoschema salinaris* Busck has more recently (1915) been reviewed by Prof. J. T. Patterson.[2] The larva of this species forms a similar gall on *Solidago sempervirens* whereas *G. gallæsolidaginis* has been found by the writer to breed in the stems of the *Solidago canadensis, serotina,* and *nemoralis.* There are points in the life-history and appearance of the galls of the two species which differ noticeably, but the adults are very difficult to distinguish.

LIFE-HISTORY SUMMARY.

The insect is single brooded. The fully formed oblong or elliptically shaped gall (Plate VIII, Fig. 3) is to be found from the latter part of July[3] on through the winter. If the galls be cut open early in July a uniformly dark colored larva with darker patches on the thorax and abdomen will usually be found in the chamber (Plate VIII, Fig. 4). The larva becomes fully grown during the latter part of July or early in August at which time it measures about 17 mm. in length. Its food for growth has been obtained by gnawing at the stem of the goldenrod from the inside, which action doubtless causes the rod to bulge outward at the feeding place and the gall to be thus formed.

[1] Busck, August, New Species of Moths of the Superfamily Tineina from Florida, Proc. U. S. Nat. Museum, Vol. 23, 1900, p. 227.

[2] Observations on the Development of *Copidosoma gelechiæ*, Biological Bulletin, Vol. 29, No. 6, December, 1915.

[3] All dates unless otherwise specified are for Ithaca, N. Y., conditions. Variations in the time of appearance of different stages in different regions are referred to later.

Following the making of the exit hole in the wall of the gall at the anterior end so that the adult may readily emerge, the larva pupates. This takes place about August 5. The dark wine colored pupa (Plate VIII, Fig. 6) measures about 12 mm. in length. It is always found head up in the gall chamber. The pupal stage covers a period of about thirty-six days (51 days in North Carolina).

The adults (Plate VIII, Fig. 7) emerge from the galls through the previously prepared exit holes during the last part of August and early September. After mating the eggs are deposited singly on the stems and lower dried leaves of the goldenrod. Oviposition begins within a few days after mating and extends over a period of two weeks. The adults live about three weeks.

The insect hibernates in the egg stage, with the eggs remaining on the rods and leaves in some instances; but usually the leaves bearing the eggs may drop to the ground; likewise the stems may fall over, so that many of the eggs may pass the winter on the ground more or less protected by various leaves and other vegetation.

Completely formed larvæ are developed within the eggs during the fall but they do not emerge until late in May of the following spring. The time of hatching varies considerably in the same locality from year to year, but it occurs regularly at the time when the new goldenrod shoots are four to six inches high.

The young and minute larva upon emerging from the egg crawls rather aimlessly about until it comes in contact with a new goldenrod shoot whereupon it crawls up the stem to the unfolding bud. It is obvious that the mortality at this time would be abnormally high as the young larvæ would frequently fail to locate a new goldenrod shoot were it not for the fact that the shoots grow directly from the old root stock. The place of hatching of the egg is therefore close to a new shoot, hence comparatively little difficulty is encountered by the larva in finding a new shoot in which to make its home.

When the larva reaches the bud end of a new rod it bores into the bud entering it from the side. Here it takes its first meal and proceeds to eat its way a short distance (one to two inches) down the center of the rod, where it remains. Feeding is continued on the inside and this, coincidentally with the growth of the rod, causes the formation of the typical gall, the chamber of which is the home

of the larva. Here the larva remains until fully grown, the gall meanwhile increasing in size until by the latter part of July the larva is mature; the rods have usually ceased growing; and the gall measures from 1½ to 2½ inches in length depending upon the species of *Solidago* upon which it is found.

DESCRIPTION.

The Adult: The two sexes are not strongly dimorphic, but they may be distinguished by their size and activity when confined in cages. The female measures 23 mm. from tip to tip of wing while the male measures only 20 mm. The forewings are dark, the anterior middle part being a reddish brown while the base and tip of the forewing shades from brown to gray. The hind wings are considerably lighter but ashy-gray in general color.

When the wings are folded their tips flare upward and the moths strongly resemble an upturned boat of which the dorsal ridge of the wings represents the keel. The wings extend slightly beyond the abdomen. The males average 10.5 mm. in length from head to tip of wings and the females 12 mm.

The Egg: The egg (Fig. 1) is more or less cylindrical but rounded at both ends and measures .3 mm. by .8 mm. in size. The chorion is delicately sculptured with numerous ridges which gives its surface the appearance of being composed of numerous delicately sunken polygonal areas. When first deposited the egg is creamy-white in color, but with the development of the embryo its color turns to yellow and finally a pale orange. During winter when the embryo is completely developed the chorion appears slightly shriveled. The writer has had occasion to section numerous eggs and has found the chorion to be tougher than that of the average lepidopterous egg.

The Larva: The newly hatched larva measures about 1.3 mm. in length and .3 mm. in width. At first it is pale green with a dark brown head and pronotal shield, but soon after commencing to feed the general color becomes brown. This uniform brown color is maintained throughout its period of growth although as it becomes full grown, four minute darker pigmented tubercles, which are arranged in the form of a trapezoid, are to be observed on each segment (Plate VIII, Fig. 5).

The first moult takes place while the young larva is secluded in the terminal bud of the goldenrod shoot and the succeeding moults (five altogether) are undergone in the gall chamber, since the larva never abandons the gall. During growth it was observed that the excrement is packed in the apex and base of the gall but mostly in the base (Plate VIII, Figs. 4, 6 and 8), the chamber always being scrupulously clean. This detritus was carefully examined for the moult skins upon a number of occasions and four head capsules representing four additional instars were always found. The last moult skin is always found either in the base of the gall chamber or adhering to the pupa (Plate VIII, Fig. 6).

The length of the instars was determined by measuring the size of the head capsules and comparing them with the size of the heads of a large number of larvæ during June and July, and further comparing them with the length of the larvæ. This data is given in Table I and indicates that the length of the instars averages 8, 8, 9, 15 and 24 days respectively although the last instar includes a semiquiescent prepupal period of about a week during which time the larva shrinks perceptibly in size. No descriptions of the instars are given since all stages are uniformly colored, a condition to be rather expected since the larva spends the last four instars of its life in complete darkness.

TABLE I. NUMBER AND LENGTH OF LARVAL INSTARS—SEASON 1914.

Instars.	Length of Larva.	Width of Head.	Average Date of Observation.	Number Specimens.
First	1.3 mm.	.3 mm.	May 30	12
Second	5.0 mm.	.4 mm.	June 8	38
Third	7.0 mm.	.6 mm.	June 16	46
Fourth	10 to 14 mm.	1.2 mm.	June 25	49
Fifth	16 to 13 mm.	1.4 mm.	July 10	41

The Pupa: The pupa averages 9.5 mm. in length. It is shiny mahogany brown in color which changes to an almost jet black (Fig. 6) just before the adult emerges. It shows no striking characteristics in which it might differ from the usual lepidopterous naked pupa.

BIOLOGY AND HABITS.

The writer has had occasion to follow the complete life-history of this gall-maker during several years and to rear the insect from the

egg to adult stage. In order to do this successfully it was first essential to observe the biology and habits of the insect very closely in its various stages. These observations proved not only interesting but will throw considerable light upon conflicting statements in literature relative to the biology of the adult.

As has been pointed out briefly above—the adult appears in late summer or early fall, deposits its eggs and then dies. The insect hibernates in the egg stage. The eggs hatch about May 16, the larvæ crawling to the new goldenrod shoots and developing in galls.

Concerning the adult, Riley (1869) says that "the moths winter over" and not the eggs, "and may be seen flying in the month of May in which month I have myself captured a specimen. When the young plants of the goldenrod are about six inches high the female moth deposits an egg in the terminal bud, or at the side of the stalk just below it, and the worm hatching from the egg works into the stalk and causes it to swell by gnawing and thus inducing the secretions towards it."

Perhaps on the basis of Riley's observations, Patterson (1915) thought that the adults of *Gnorimoschema salinaris* must deposit their eggs normally in the spring. Speaking of the parasite *Copidosoma gelechiæ* Patterson says "the parasites must winter over in the imago state; otherwise they would not be able to parasitize the normal or spring eggs of *Gnorimoschema.*" On the other hand Patterson did secure some eggs in fall from *salinaris* moths which were confined in cages, which he was inclined to believe developed parthogenetically although the moths were confined with males. He further makes the statement that "*G. gallæsolidaginis* from the galls of *S. canadensis* in western Ohio likewise drops several eggs soon after emerging from the pupa in September." Patterson questioned the development of the fall eggs of this species into larvæ under normal conditions, solely because of difficulties the young larvæ would have in withstanding the winter or in finding a new shoot of the goldenrod in spring.

The writer has never encountered any difficulty in securing eggs from adults of *gallæsolidaginis* in fall. Moths have been caged time after time in glass cylinders with cheese cloth top with living goldenrod stems, and in large outdoor cages 5 x 5 x 4 feet in size built over clumps of goldenrod. In this way thousands of eggs have been secured at will.

Emergence, Mating and Oviposition of Moths: The moths emerge from the galls at night through their previously prepared exit holes. In some instances moths for some reason or other, probably because of an improperly prepared exit hole, are unable to escape from the galls.

Female moths begin to deposit eggs within four or five days after emergence when they have been previously confined with males. The eggs are deposited singly, although two or three may be placed close together and perhaps mass-like in actual contact with each other. These are placed on both surfaces of a leaf but usually on the under side and preferably on one that is dried; and on the stems among the hairs. During oviposition which occurs at night the female is very active, flitting about in cages, crawling up the stem, or jumping from one leaf to another. The placing of an egg requires from eight to ten seconds and during the process, two segments of the abdomen ordinarily hidden are extruded, and the egg emerges from the tip; meanwhile the moth frequently twists or swings the tip of the abdomen from side to side in search of a crevice, such as the point of attachment of a leaf to a stem, or the vein of a leaf, and, finding such a crevice or place against which the abdomen may rest for an instant, the egg is deposited. As the egg is extruded it appears wet and glistening with a secretion which probably serves to fasten it to the leaf or stem. The moth may fly away, adjust its position only slightly, or merely move the tip of the abdomen before depositing another egg. An average of about sixty eggs is deposited by one female although one moth deposited a total of ninety-six eggs in an outdoor cheesecloth cage over a period of seven nights.

During the day the moths rest secluded, apparently hidden by their color resemblance to the dried leaves of the goldenrod, within the curled leaves or among the florets. When disturbed they quickly attempt to seclude themselves, and do not fly about for any length of time.

Moths have been observed to partake of nourishment in the form of sweetened water when placed in indoor cages. It may be this factor which causes females to deposit a greater average number of eggs in indoor cages than under the semi-natural conditions of outdoor cages.

Eggs have been commonly and regularly found in fall under natural field conditions so that there is no doubt but that oviposition in fall is normal for this species.[1] In order to secure further evidence, however, certain experiments in burning over small areas of goldenrod in fall were carried out with a view to determine whether galls would develop upon the new shoots in spring in the burned-over areas. This was done in two seasons (during November) and resulted in the burning of the old goldenrod stems and leaves in restricted areas which had been abundantly infested with galls that year. The new shoots which grew in the burned-over areas did not develop galls the following spring, while the new shoots of adjacent areas not burned over did develop galls. These experiments may be commonly substantiated on a large scale in North Carolina where fires sweep through woods and about their edges. Goldenrod shoots growing out the following spring are inevitably free of galls in the burned-over areas if the burning has been thorough. Moreover, it is further apparent that spring overflows or freshets of streams prevent the eggs in the territory covered by the freshet from hatching, by drowning the young larvæ in the eggs or perhaps by covering them with mud. The writer has had occasion to observe during summer after an overflow in spring, that goldenrod in the area not covered by the freshet was infested with galls while the flooded area showed the goldenrod free of galls; the line of high water was identical with an imaginary line between the gall-free and infested areas of goldenrod.

Embryonic Development: Immediately after deposition the eggs begin to develop. Under Ithaca, N. Y., conditions this requires about 26 days while in North Carolina the period is lengthened to about 35 days. The overwintering egg therefore contains a fully formed larva partially coiled within the egg shell.

The question of parthenogenesis in *Gnorimoschema* has been raised by Patterson who figures[2] a section of an egg of *salinaris* which he states was deposited by a female not associated at any time with males. Apropos of this, some of the writer's experiments along this line with *gallæsolidaginis* may be of interest. Unfertilized females were upon several occasions separately caged, and frequently they

[1] This is certainly the time for the species in Vermont, New York and North Carolina.

[2] *Loc. cit.*

have deposited or dropped some eggs; but these developed only partially and never any semblance of an embryo. Moreover such eggs were always deposited eight or nine days after those of a similarly aged but fertilized female. Unfertilized eggs are therefore probably dropped only abnormally, and parthenogenesis in *gallæsolidaginis* does not occur.

Hatching of Eggs: According to records of three years the eggs hatch in North Carolina between March 22 and April 5. The hatching date for New York has not been secured but when an early instar under North Carolina conditions is compared with a similar instar in New York, it can readily be determined that the eggs must hatch in New York around May 16.

The first determination of the time of hatching of the eggs followed the failure of three successive winters in attempts to keep them through the winter under semi-natural conditions. During the fourth winter of experiment, eggs[1] deposited regularly on dried leaves and stems of goldenrod in fall were carried through by placing these leaves and parts of stems in small shell-vials stoppered loosely at both ends with cotton; the vials were in turn placed in larger vials similarly stoppered. This method solved the problem of continued excessive moisture previously encountered. The eggs hatched normally, the larvæ producing galls which were visible on the new goldenrod shoots at the same time that the galls of a similar size were visible in the field. In the two following years the date of hatching in vials was again closely compared with the time of hatching in the field, and the dates found to accord.

Growth and Habits of Larvæ: The process of hatching and location of a new goldenrod shoot by the young larva has been watched continuously for as much as six hours at a time. The young larva which measures but 1.3 mm. in length seems to crawl aimlessly about on blades of grass or over earth, and the watching of them in the hopes they will find a goldenrod shoot is at times most exasperating. But once the larva comes in contact with a goldenrod shoot, which at this time is four to five inches in height, it proceeds to crawl up the shoot to the bud end, crawl about on the tender leaflets for a little

[1] These eggs had been oviposited in by the polyembryonic parasite *Copidosoma gelechiæ* and it was primarily intended to keep these particular eggs for rearing of the larvæ in spring.

while and finally eats its way into the bud from the side. It remains in the bud for five to seven days where it feeds (and undergoes its first moult), during which time its presence may be externally detected by the finding of its excrement among the leaves of the bud; and then burrows its way down the center of the stem. The leaves which compose the bud while the larva is within show signs of the feeding of the larva when they grow out, some having irregularly frayed edges while others are full of small holes.

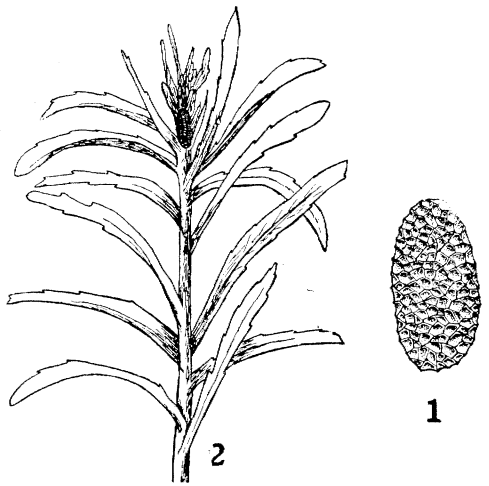


Fig. 1.—Egg. × 28.

Fig. 2.—Small gall beginning to form just below the bud of goldenrod shoot.

The second stage larva eats its way down the stem for a distance of two to three inches. This distance determines the comparative position of the gall on the rod when fully grown. Here it remains and within a few days, after it has fed at one point by gnawing on the interior of the stem, the gall begins to develop (Fig. 2). The continued feeding doubtless causes a stimulation of the plant tissues in the vicinity of the larva, for the gall increases to a size on each species of *Solidago* proportionate to the amount of feeding done by the larva. Thus when the larva dies within the gall before becoming fully grown (this happens frequently because of parasites), it has been observed that the growth in size of the gall also ceases. Occasionally two larvæ

happen to enter the bud of the same stem and two galls are thereupon produced on such a rod.

After the larva has fed for ten days or so in the gall, it packs the accumulated excrement mixed with a little silk in the apex of the chamber and thus seals its entrance passageway. Subsequent excrement is similarly packed in the base of the gall chamber, the inside being always kept scrupulously clean.

When the larva is about three fourths grown it begins to eat a small channel toward the outside of the gall at the anterior end (Plate VIII, Figs. 4 and 6) which is continued until the very outside layer of the stem is reached. Later the outside layer is cut and used, together with silk secreted by the larva, to form a peculiar circular plug (Plate VIII, Fig. 3) measuring 2 mm. in diameter and 1.6 mm. thick, which is so constructed and placed that it can readily be pushed outward from within but not inward from without. This serves as an exit hole for the adult.

The larva ceases to feed to any extent about July 20 at which time it measures around 14 mm. in length. For a period of a week to ten days it lies semiquiescent within the gall, but during this time it cleans out the gall thoroughly, packing all excrement in the base, and then lines the gall with a thin layer of silk. Following this it pupates, the last larval skin sometimes remaining attached to the caudal end of the pupa (Plate VIII, Fig. 6).

The pupal stage covers a period of about one month at Ithaca, N. Y. (August 5 to September 10).

The moth upon emerging from the pupal shell crawls to the apex of the gall, and remains there until the wings are completely developed and dried. It then approaches the plug of the exit hole, exudes a drop of secretion which allows the plug to be readily pushed aside, and emerges from the gall.

Seasonal Occurrence: The writer has been privileged to determine the time of appearance of the various stages in three widely separated regions, viz., Williamsville, Vermont,[1] Ithaca, New York, and Raleigh, North Carolina. The insect is single brooded in each region and

[1] Many thanks and appreciation are due Mr. S. A. Merrifield, of Williamsville, Vermont, who frequently sent me galls of this species and made some biological observations in this locality which have been used in this paper.

there is a very close correlation between the development of the insect and its host plant, the goldenrod.

The time of hatching of eggs occurs in each region when the goldenrod shoots are four to six inches high. This as seen in Table II begins as early as March 26 in North Carolina and probably occurs gradually later as one moves northward, until as far north and east as Vermont, the average date of hatching is as late as May 20. The length of the larval stage extends over 150 days in North Carolina, 81 days in New York and 71 days in Vermont. Similarly the pupal stage is longer in the "warmer" regions, being increased from 24 days in Vermont to 51 days in North Carolina. We thus see that the activity of the larvæ in Vermont begins late (May 20) and ends early (August 23), covering a period of 95 days; at Ithaca, N. Y., it begins slightly earlier (May 16) than in Vermont and ends slightly later (Sept. 10), covering a period of 117 days; while in North Carolina hatching is much earlier (March 26) and emergence much later (October 13), covering a period of 221 days. This not only holds true for this insect but for at least one of its primary parasites, *Copidosoma gelechiæ*, as well.

These data are in a measure an exception to the theory often applied to insects, that the warmer the climate the more rapid the growth and the greater the number of generations.

TABLE II. APPEARANCE OF STAGES AND THEIR LENGTH IN VARIOUS REGIONS.

Region.	Date of Hatching of Eggs.	Length of Larval Stage.	Date of Maximum Pupation.	Length of Pupal Stage.	Date of Maximum Emergence.
Williamsville, Vt.	May 20	71 days	July 30	24 days	Aug. 23
Ithaca, N. Y.	May 16	81 days	Aug. 5	36 days	Sept. 10
Raleigh, N. C.	Apr. 3	150 days	Aug. 23	51 days	Oct. 13

PARASITES.

An exceptionally high percentage of the individuals of all stages is attacked by hymenopterous parasites and their detailed study would afford a fascinating problem. Hyper-parasites and inquilines are also commonly bred from the galls. In two instances two species of parasites (*Copidosoma gelechiæ* and *Scambus pterelas*) were reared from a single larva.

The writer has devoted considerable attention to the study of some of these parasites, particularly the biology and development of the polyembryonic parasite *Copidosoma gelechiæ*.[1] Only brief references will be made here to the species[2] bred.

Eurytoma sp. (probably *bolteri* Riley): An external parasite of the larva whose egg is either placed on the host larva or deposited in the gall chamber and eventually coming in contact with the host. Some of the parasite larvæ pupate in late summer and produce adults which emerge from the galls while other larvæ remain naked in the gall over winter and produce adults the following spring. Common at Ithaca, N. Y., present in Vermont and North Carolina.

Pleurotropis sp.: Parasite of *Eurytoma* sp. with a life-history similar to that of its host. Five to twelve larvæ commonly attack one host larva. Ithaca, N. Y., and Vermont.

Copidosoma gelechiæ How.: This primary parasite deposits its egg in the host egg. The host larva develops normally until just before pupation when it dies. An average of around 165 individuals of the parasite are developed in one larva from one parasite egg. The parasites pupate in the host carcass about August 10, emerge as adults nearly a month later and then escape from the gall. Common at Ithaca, N. Y., Williamsville, Vermont, and fairly common in North Carolina.

Calliephialtes notanda Cress.: Parasite develops in larva devouring it so that it does not pupate. Larva pupates in the gall in elongate brown cocoon made of tough silk, from which the adult emerges in late summer. Very common in North Carolina, present at Ithaca, N. Y.

Scambus pterelas Say: Parasite larva destroys the host larva and pupates naked in gall chamber. Adult emerges from gall Aug. 12–24. Bred fairly common at Ithaca, N. Y.

Phaeogenes gelechiæ Ash.: Emerges from host pupa and then from gall. Common at Ithaca, N. Y.

Campoplex dimidiatus Cress.: Adult emerges from tough brown white banded cocoon spun inside gall chamber. Overwinters in cocoon and adult emerges late March. Ithaca, N. Y. (rare).

[1] To be issued in December 1922 number of the Journal of Morphology.

[2] The parasites were determined by Messrs. A. B. Gahan and S. A. Rowher of the U. S. Nat. Museum through the kindness of Dr. L. O. Howard and in part by the writer.

Microgaster gelechiæ Riley: Adult emerges from gall and white silken cocoon within in spring. Common in North Carolina and present at Ithaca, N. Y.

At least two other species of parasites have been reared but not as yet determined. One species is a gregarious braconid, the other is probably *Pseudacrias sexdentatus* Girault.

EXPLANATION OF PLATE VIII.

FIG. 3. Two fully grown galls. Plug pushed out to allow the escape of moth in the right gall revealing the exit hole while the gall to the left shows the plug in place. Natural size.

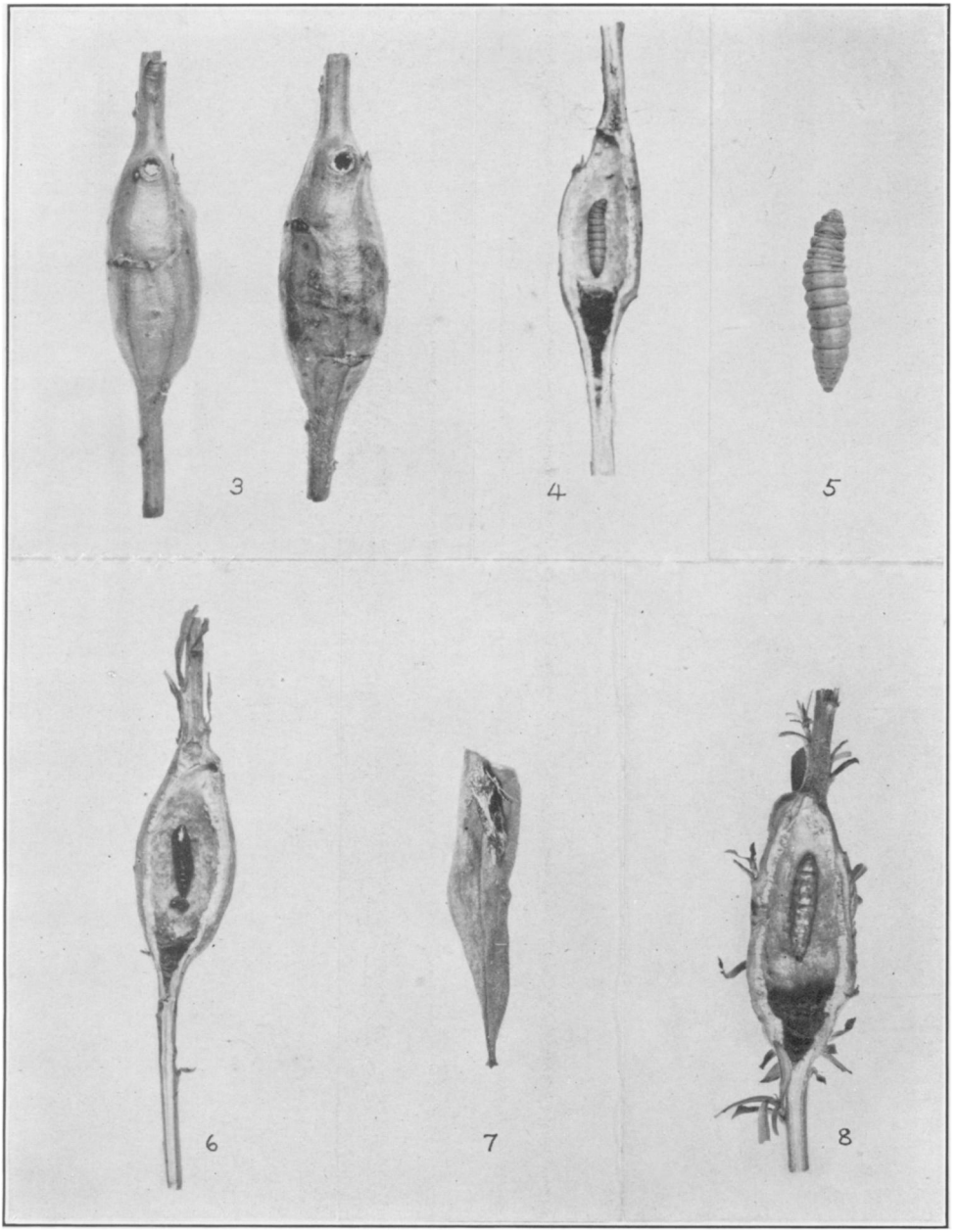
FIG. 4. Nearly grown larva in gall cut open. Note passageway leading to exit hole at apex of the gall on the left, and excrement packed in base of gall chamber. Natural size.

FIG. 5. Full grown larva. × 2.5.

FIG. 6. Pupa in gallchamber. Natural size.

FIG. 7. Adult on goldenrod leaf. Natural size.

FIG. 8. Larva parasitized by *Copidosoma gelechiæ* in gall chamber.



GNORIMOSCHEMA.